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Adaptive strategies of weevil larvae in the superparasitized acorns of the Oriental white oak, *Quercus aliena* (Fagaceae)

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Abstract: Acorns of oaks are usually attacked by weevils. Although the interaction between acorns and weevils has been well studied, how acorns affect the fitness of weevil larvae remains unclear. In this study, we attempted to investigate the evolutionary adaptation of weevils to the development of acorns through carefully investigating the seed fall processes and the characteristics of larval emergence from the trapped acorns of the Oriental white oak, *Quercus aliena*. Our results indicated that seed crop of *Q. aliena* was 51.92 ± 29.26 nuts/m^2 with an infestation rate estimated of 42.4% in 2009. The infested acorns were much larger than the sound ones. About 65% of the infested acorns were superparasitized by weevil larvae. Weevil larvae emerged earlier were much larger than those exited later from infested acorns after seed fall. Early emerged weevil larvae were much larger than those coming out later from the same individual superparasitized acorn. Weevil larvae parasitized in the early abscised acorns were smaller than those in later abscised ones. Our results demonstrated that dry weight per weevil larva was decreased significantly with the increase in the number of weevil larvae in single acorn. The number of weevil larvae was closely and positively correlated with length and maximum width of acorns, respectively. Although the fitness of weevil larvae was reduced in the superparasitized acorns, a preference of female weevil for larger acorns to oviposition may counter this disadvantage. Our results may suggest that smaller acorns may benefit from superparasitization because large acorns attract female weevils to oviposit more eggs.

Key words: *Quercus aliena*; acorn; weevil; superparasitization; larval fitness

1 INTRODUCTION

For many plants producing large-sized seeds, the damage caused by insect predators is often very extensive prior to seed dispersal (Crawley, 1992; Hulme and Benkman, 2002; Yu *et al.*, 2003). To cope with insect herbivory, plants evolve a number of morphological and chemical characteristics that serve as defense mechanisms against seed predators and dispersers (Harborne, 1991; Steele *et al.*, 1993; Hughes and Vogler, 2004; Bonal *et al.*, 2007; Yi and Yang, 2010). Therefore, the interactions between plant seeds and their seed predators provide a model system to explore how seed predators interact and evolve in response to plant defense system.

Weevils of the genus *Curculio* are the major predator of various oak species (Downs and McQuilken, 1944; Collins, 1961; Kearby *et al.*, 1986; Sun *et al.*, 2011) and the most studied insect predators affecting tree regeneration (Crow, 1988; Andersson, 1992; Crawley, 1992; Siscart *et al.*, 1999; Riccardi *et al.*, 2004). Several studies have shown that the acorns infested by insects experience lower germination rates (Soria *et al.*, 1996; Siscart *et al.*, 1999; Branco *et al.*, 2002; McDonald *et al.*, 2003), indicating that pre-dispersal acorn predation by insects is one of the constraints for the sexual regeneration of oaks (Oliver and Chapin, 1984; Oak, 1993; Crawley and Long, 1995; Yi and Zhang, 2008; Espelta *et al.*, 2009b; Hou *et al.*, 2010). Because of poor regeneration of many oak species, researchers have made great efforts to investigate the ecological consequence of the loss of acorn production by moths (*e. g.*, *Cydia*) and weevils of the genera *Curculio* (Jones, 1959; Gibson, 1964, 1971; Oliver and Chapin, 1984; Lewis, 1992; Fujii, 1993; Scutareanu and Roques, 1993; Crawley and Long, 1995; Kelbel, 1996; Fukumoto and Kajimura, 1999; Yu *et al.*, 2001; Yi and Zhang, 2008). However, there are few studies investigating the constraining effect of acorns on weevil larvae and adaptation of weevil larvae to acorn production (Yu *et al.*, 2003; Bonal *et al.*, 2007; Bonal and Muňoz, 2008; Espelta *et al.*, 2009a; Yi and Yang, 2010). Acorn-producing Oriental white oaks, *Quercus aliena* (Fagaceae), are commonly grown in the secondary and natural forests in

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temperate forest ecosystems of China, and thus are valuable seed sources for forest restoration. However, acorns of *Q. aliena* usually suffer from superparasitism by weevil larvae (Liu *et al.*, 2010; Yi and Yang, 2010), suggesting that one single acorn will attract one female weevil to lay much more eggs or a few females to lay eggs into the same acorn (termed as superparasitism) (Bai and Mackauer, 1992). Superparasitism definitely provokes an increase in the number of larvae per acorn (Bonal and Muňoz, 2008), consequently decreases the likelihood for a larva to finish its development because of increasing sibling competition for limited food. Hence, the interaction between acorn production and acorn infestation by insects would be a complicated evolutionary process in acorns of *Q. aliena*. Maintaining a higher fitness of weevil larvae and ensuring following regeneration maybe involve adaptive strategies to acorn production.

In 2009, we carried out a study with *Q. aliena* tree and its more prevalent pre-dispersal seed predator (chestnut weevil *Curculio davidi*), a specialist insect species whose larvae develop inside the acorns. The seed crop in 2009 in the study area was likely to be a medium masting year because fewer acorns were trapped in 2008, 2010 and 2011 (Liu *et al.*, 2010; Lei, 2012). We specifically attempted to answer four questions: (1) whether there is a positive relationship between the number of weevil larvae and the size of the acorns; (2) whether there is a negative relationship between the number and the size of weevil larvae in the superparasitized acorns; (3) whether there is a positive relationship between the size of weevil larvae and emergence order from acorns; and (4) whether there is a negative relationship between the size of weevil larvae and acorn abscission. We made special efforts to demonstrate the adaptive strategies of weevil larvae to superparasitism in acorns.

2 MATERIALS AND METHODS

2.1 Sampling sites

The study was conducted in Tianchishan Mountain (1 400 m a. s. l., 33°45′ – 33°85′N, 111°75′ – 112°45′E) belonging to Funiushan Mountain systems in central China, located in a transition belt between the north subtropical and warm zones. The annual mean temperature is 17℃, and the annual mean rainfall is 812 mm. The vegetation is dominated by deciduous *Q. variabilis* and *Q. aliena* secondary forests, mixed with other broad-leaved tree species, *e. g.*, *Q. serreta*, *Castanea mollissima*, *C. seguinii*, and *Diospyros kaki*. The shrubby understory is diverse and rich in endemic taxa (*Corylus* spp.) (Liu *et al.*, 2010). The stand area of this study is more than 4 hm^2 with the abundance of *Q. aliena* trees more than 70%. The average diameter of at breath height (DBH) of labeled *Q. aliena* trees ranges from 25 – 30 cm and the canopy height is 15 m on average.

2.2 Study species

Q. aliena is the most widespread temperate tree species in China. Its seed crops can be very large although with a strong inter-annual variability (Liu *et al.*, 2010). Acorns of *Q. aliena* are eaten by a large variety of animals, including insects and small rodents (Liu *et al.*, 2010). The embryo is located at the apical end of the acorn. Most seed biomass is composed by the two large cotyledons, which constitute the reserves for seedling development. The chestnut weevil *C. davidi* is the most prevalent pre-dispersal consumer of *Q. aliena* acorns (Liu *et al.*, 2010), while larvae of moth species are seldom found in these acorns. Like other borer insects, weevils attack acorns only when still attached to the parent trees.

2.3 Survey of seed rain

Twenty four *Q. aliena* oak trees were randomly chosen and labeled in our study areas in 2009. Acorns were collected using 24 seed traps that were placed under the oak canopies. Seed traps, hanged from the lower branches to avoid predation from terrestrial vertebrate predators, were designed and randomly located to capture acorns (Skalski, 1987). Avian predation is regarded as less influence on potential losses of acorns because few bird species was witnessed in the experiment sites during our survey, and most of them are small-sized passerines unable to swallow the entire acorns. A 1 m × 1.2 m polyester net (2 mm mesh) was fastened on a 0.5 m^2 metal frame to make a concave seed trap with an opening of 0.5 m^2 and 0.3 m in depth, preventing acorn rebounding after falling. The frame was set on a thin wooden rod about 1.2 m above the ground to prevent predation by terrestrial vertebrates. Traps were established to catch acorns and other debris while letting rainfall easily pass through. Seed traps were set up 1 – 2 m away from the tree trunk under the crown of the selected oak trees just before acorns ripened. The number of traps per tree was proportional to its canopy surface, in all of them it was covered between 1.5% – 2% of the canopy (Pulido and Díaz, 2005). Traps were left in place until all ripe acorns had fallen from the trees.

2. 4　Acorn classification and pre-dispersal predation by insects

Seed traps were sampled periodically from the beginning of seed fall. First acorns were trapped on 28 August in 2009, and from that date all seed traps were checked every day until seed rain ceased in late September. At each visit, traps were emptied and their contents were taken to the laboratory and deposited separately. After the length, width and fresh weight of each acorn collected every day were measured, the sound and infested acorns were consecutively numbered and individually placed indoors in plastic plates with 48 grids (4 cm × 3 cm × 3 cm) opened above, which were kept outdoors and covered with a 0. 5 mm plastic mesh to avoid predation from birds or rodents. Legless weevil larvae could not climb or escape from the grids. Acorns were checked daily to detect and count the number of weevil larvae exited from acorns (number of larvae of Lepidoptera were neglected due to very low level of infestation rate), all larvae were oven dried for 48 h at 70 – 80℃ and then weighted to the nearest 0. 1 mg using a precision balance. At the same time, the emergence position and exit order of each weevil larva were recorded, and the duration from larval emergence to the beginning of seed rain or the day when the acorn was collected were also calculated, respectively. After the last larva had been registered, the number and site of emergence holes per acorn and the number of weevil larvae escaped from per acorn were cumulatively measured.

To identify weevil species in our study, larvae collected from acorns of *Q. aliena* in 2007 and 2008 were placed in glass bottles filled with aboriginal soil. The bottles were checked during the following 2 years to identify the weevil adults emerged from the bottles. All individuals from both 2007 and 2008 cohorts (85 and 114, respectively) were identified as *C. davidi*. We also sampled adults at the experimental oaks by branch shaking during the 3-year studies. All the adults captured (76) were *C. davidi* as well.

2.5　Statistical analysis

Linear regression was used to evaluate whether there was a negative or positive relationship between the number of weevil larvae and acorn traits (length and maximum width). Linear regression was also used to analyze whether average dry weight per weevil larva depended on acorn size, the number of growing larvae, or the emergence time from acorns. A general linear model (GLM) was used to test the effect of emergence order on the dry weight per weevil larva. Independent Samples *T* Test was used to see the difference in seed size (length and maximum width) of sound acorns and infested acorns.

3　RESULTS

3.1　Seed rain of *Q. aliena*

Our results indicated that the first acorn of *Q. aliena* was recorded on 28 August and the seed rain ceased on 28 September (Fig. 1). The seed crop of *Q. aliena* was 51.92 ± 29.26 acorns/m^2. We totally trapped 623 acorns, of which 225 of them were sound, 264 were infested and 134 were aborted. Acorn volume was 1.94 ± 0.61 cm^3 on average. The infested acorns (2.29 ± 0.42 cm^3) were much larger than sound ones (1.59 ± 0.32 cm^3) ($t = -2.533$, $df = 16$, $P = 0.022$), indicating preference of female weevil for larger acorns to oviposition. The infestation rate of the overall acorns was estimated at 42.4%. More than 35.1% of infested acorns contained single weevil larva, however, 17.6%, 14.5% and 13.5% of damaged acorns were parasitized by 2, 3 and 4 weevil larvae, respectively (Fig. 2).

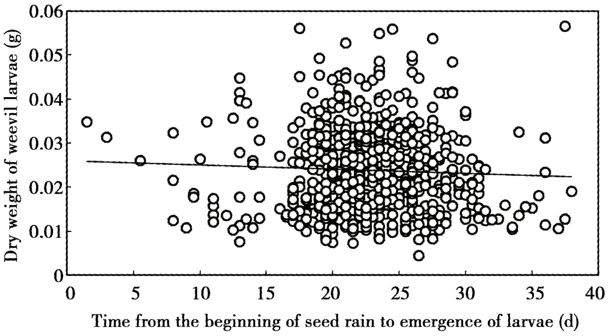

Fig. 1　The emergence characteristics of weevil larvae from acorns of *Quercus aliena*

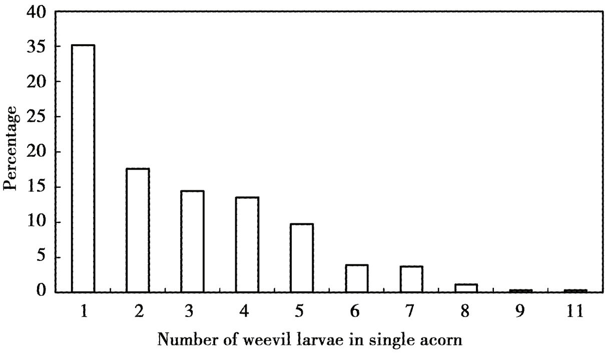

Fig. 2　Percentage of acorns of *Quercus aliena* infested by weevil larva

3. 2　Larval size related to emergence time and superparasitization

Although weevil larvae emerged earlier from the infested acorns were not larger than those exited when considered from the beginning of seed rain ($r^2 = 0.098$, $F_{1,57} = 6.175$, $P = 0.016$) (Fig. 1), the early emerged weevil larvae were much larger than those that came out later from the single superparasitized acorn ($F = 3.555$, $df = 4$, $P = 0.007$), with the 4th and 5th individuals much smaller than the 1st, 2nd and 3rd ones (all $P < 0.05$) (Fig. 3). Weevil larvae parasitized in prematurely abscised acorns were smaller than those in the fully developed acorns ($r^2 = 0.568$, $F_{1,23} = 30.281$, $P < 0.001$) (Fig. 4). The size of early trapped infested acorns was much smaller than that of later trapped ones in terms of acorn length and width ($r^2 = 0.576$, $F_{1,25} = 33.895$, $P < 0.001$; $r^2 = 0.405$, $F_{1,25} = 17.028$, $P < 0.001$) (Fig. 5). Dry weight per weevil larva was decreased significantly with the increase in the number of weevil larvae in single acorn ($r^2 = 0.017$, $F_{1,702} = 12.224$, $P < 0.001$) (Fig. 6). The number of weevil larvae was closely and positively correlated with length and maximum width of acorns, respectively ($r^2 = 0.589$, $F_{1,8} = 11.471$, $P = 0.010$; $r^2 = 0.760$, $F_{1,8} = 25.392$, $P = 0.001$) (Fig. 7), indicating that female weevils prefer larger acorns for superparasitization. Weevil larvae tended to emerge from the basal end of acorns infested by less than 3 larvae ($\chi^2 = 7.980$, $df = 2$, $P = 0.018$), however, emergence holes were more likely to be found at the apex of acorns superparasitized by more than 3 larvae ($\chi^2 = 2.420$, $df = 2$, $P = 0.298$) (Table 1).

Table 1 Distribution frequency of emergence sites in acorns infested by more or less than 3 weevil larvae

Acorn type	Emergence site		
	Apex	Middle	Base
≤3 larvae	27.59%	25.86%	46.55%
>3 larvae	37.47%	25.52%	37.01%

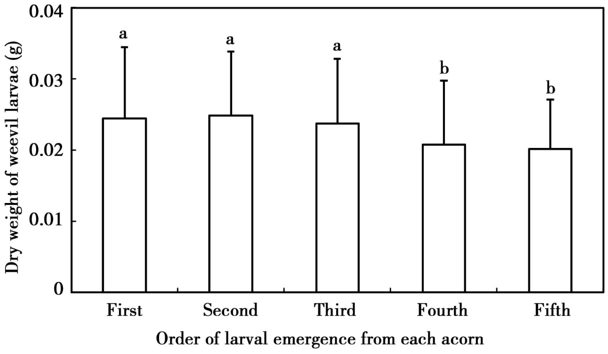

Fig. 3 Variation in dry weight of weevil larvae with emergence order from single acorn of *Quercus aliena*

Data are expressed as mean ± *SD* (GLM One-way ANOVA). Different letters on the histograms indicate significant difference at $P = 0.05$ level. The same below.

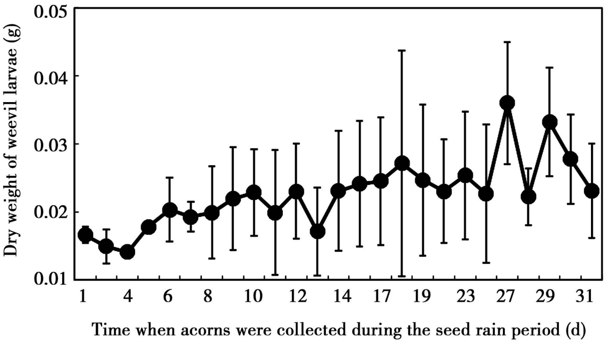

Fig. 4 Variation in dry weight of weevil larvae in acorns of *Quercus aliena* collected during the seed rain period

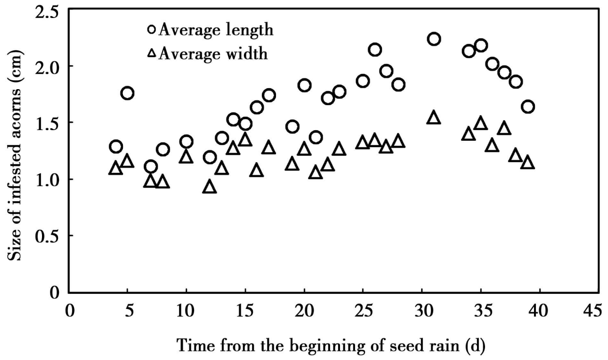

Fig. 5 Variations in size of the infested acorns of *Quercus aliena* collected during the seed rain period

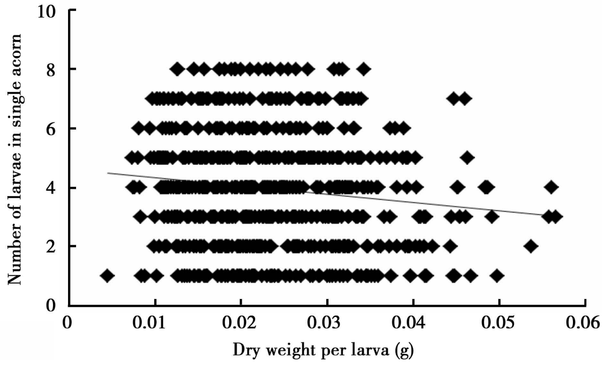

Fig. 6 Relationship between average dry weight and number of weevil larvae per acorn of *Quercus aliena*

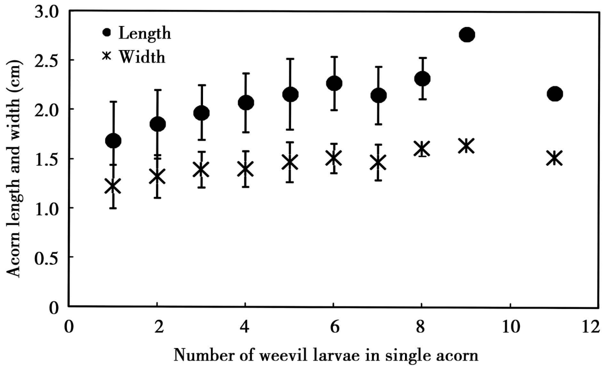

Fig. 7 Variations in length and width with the number of weevil larvae in the infested acorn of *Quercus aliena*

4 DISCUSSION

The characteristics of larval emergence from acorns were reflected in the life history of the weevil, *C. davidi*. Most adult weevils began to lay eggs in early August, with a peak oviposition activity in mid-August, continuing into early September, generally reflecting the same life history patterns of other weevil species, *C. dentipes* and *C. arakawai* in temperate areas in China (Cheng and Hsu, 1959; Chen, 1988), but a little bit different from *C. sikkimensis* (Kim *et al.*, 2008). We found that larval emergence was concentrated in mid-September and varied from 1 to 38 days after falling of acorns (Fig. 1). Oliver and Chapin (1984) recorded similar larval emergence of *C. fulvus* Chittenden in the live oak, *Q. virginiana* Miller, in Louisiana. A similar larval emergence was also found in *C. dentipes* in acorns of *Q. liaotungensis* (Yu *et al.*, 2003). However, weevil larvae emerged from early abscised (or trapped) infested acorns were much smaller than those emerged from later acorns (Fig. 4), indicating that larvae inside the later infested acorns grew to a larger size compared with those developing inside the early infested acorns, which very frequently and completely consumed the cotyledons and suffered food deprivation due to their small sizes (Fig. 5). Larvae must complete their development feeding inside a single acorn, thus, they do not get any benefit from the early infested acorns dropped from the oak trees. However, this fact could not explain superparasitism in later abscised infested acorns because the number of adults by the trees will increase (Fernández-Carrillo *et al.*, 2002) and the availability of uninfested acorns will decrease. The negative consequences for larval size suggest that the early abscission of the infested seeds could be a plant defense, as it can constrain growth of larvae.

Superinfestation induces an increase in the number of larvae per acorn thus increasing sibling competition for food resources (Bonal and Muñoz, 2008), which has a negative effect on larval size. In our study, larval size was significantly constrained in superparasitized acorns of *Q. aliena* (Fig. 6). Hence, superparasitism in acorns could limit the food availability for larval development, constraining larval size and fecundity and reducing the fitness prospects of these insects. Larval size has been shown to be strongly related to several key fitness variables such as survival of diapause larvae, adult size or female potential fecundity (Bonal and Muñoz, 2008). Our results demonstrated that there was a negative relationship between the number and the size of weevil larvae in the superparasitized acorns, supporting the results of Desouhant *et al.* (2000). Larval size is a widely acknowledged key life history trait of insects (Engelmann, 1984; Fox *et al.*, 1996; Fox and Savalli, 1998). Larval size in acorns parasitized by less than 3 weevil larvae was less likely to be constrained. However, larval size in acorns parasitized by more than 3 weevil larvae was significantly constrained. Superparasitism might have negative consequences for insect fitness as it constrains larval size. Still more larvae emerged earlier from superparasitize acorns (the former 3 larvae) were much larger than those that emerged later (Fig. 1), indicating less conspecific competition for food among early emerged larvae. More weevil larvae were forced to emerge from apex of acorns when superparasitized by more than 3 larvae (Table 1), indicating more conspecific food competition in acorns and resulting in much more possibilities of embryo death. Hence, there seems to be an optimum window of weevil larva number (3) for superoviposition by female weevils after the acorns reach a certain size. Despite superparasitism frequently occurred in acorns of *Q. aliena*, the number of weevil larvae was positively correlated with acorn size and mass. These correlations predict a preference of female weevils for larger acorns to oviposition; smaller acorns may escape from superparasitization because large acorns attract female weevil to oviposit more eggs.

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槲栎超寄生橡子内象甲幼虫的适应对策

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摘要：栎属植物的橡子常常受到象甲的侵害，对橡子存活产生影响，但有关橡子对象甲幼虫适合度影响的研究尚未见报道。本研究旨在通过对槲栎 *Quercus aliena* 种子雨进程以及象甲幼虫逃逸过程的调查，研究二者之间的进化适应关系。结果表明：当年槲栎的种子产量为51.92±29.26粒/m^2，虫蛀率达到42.4%。虫蛀的橡子中65%以上被象甲超寄生，且显著大于完好的橡子。在种子下落过程中，早期从橡子中逃逸的象甲幼虫要比后期逃逸的大。对某一超寄生的橡子而言，首先逃逸出的象甲幼虫要比随后逃逸的幼虫大。另外，从早期脱落的橡子中逃逸的幼虫明显小于后期脱落的橡子。象甲幼虫的干重随着橡子内象甲幼虫数量的增加而显著下降。象甲幼虫寄生数量与橡子的长径和短径呈现明显的正相关关系。尽管超寄生降低了象甲虫的适合度，但雌性成体象甲产卵过程中偏好选择大橡子在一定程度上可以减少这种不利影响。因此，小橡子可能更容易逃脱象甲的超寄生而获得较大的存活机会。

关键词：槲栎；橡子；象甲；超寄生；幼虫适合度

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